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Upper Pliocene and Lower Pleistocene Bird Remains from Poland

[Pp. 531—566, Pls. XXIII—XXIV and 3 text-figs.]

Górnoplioceńskie i dolnoplejstoceńskie szczątki ptaków z Polski

Верхнеплиоценские и нижнеплейстоценские останки птиц из Польши

Abstract. The author describes the Villafranchian bird faunas from Polish fossil localities Węże I (4 species), Rębielice Królewskie I and II (17 species) and Kadzielnia (2 species). Among them 2 species and 4 subspecies are new: *Lagopus lagopus atavus* n. ssp., *Tetrao conjugens* n. sp., *Francolinus* (*Lambrechtia*) *minor* n. sp., *F. capeki wenzensis* n. ssp., *F. capeki villanyiensis* n. ssp. and *Athene noctua veta* n. ssp. A detailed morphological description of the remains is given and the systematic and stratigraphic position of the particular forms is discussed.

CONTENTS

I. INTRODUCTION

The materials described were collected in 3 localities in Southern Poland (Kraków-Wieluń Jurassic Ridge and the Holy Cross Mountains) and are kept in the collection of the Institute of Systematic and Experimental Zoology of

Polish Academy of Sciences, Kraków. I am very indebted to the director of this Institute, Prof. Dr. K. Kowalski, for having intrusted me with the work on these materials.

The bird fauna the Pliocene-Pleistocene boundary of Europe is insufficiently known and therefore of considerable interest. I explained in another place the difficulties of such studies (see Jánossy, 1965). The transitional period between the Pliocene and Pleistocene is characterized by the vanishing of the typical Tertiary faunistic elements (their descendants are today chiefly etiopic-oriental species) and by the gradual emergence of the recent avifauna of Europe. Therefore there existed at that time many forms standing morphologically close to the present European ones, but in spite of this fact we must take into account many subtile osteological differences against the representants of recent populations. These differences are often only of statistical character, and unfortunately the recent comparative material as well as the fossil one are in many cases not numerous enough for such investigations.

The above mentioned difficulties are augmented by the fact, that intact bones occur in small numbers only among the findings. The majority of them are broken or generally of very poor condition due to the activity of birds of prey, — the predators of those times — and moreover to the erosion in the sediment as well.

The determination of the geological age of the faunas is not quite unambiguous. Among the three localities Węże, on the base of small mammal fauna, can be dated as the Uppermost Pliocene („Lowest Villafranchian") and is the oldest one. Rębielice Królewskie is younger, about on the „boundary" of the Pliocene and Pleistocene („Middle Villafranchian"). Kadzielnia is clearly the youngest one, in our actual conception distinctly Lowest Pleistocene („Upper Villafranchian") (see Kowalski, 1958, 1960a, 1960b, etc.).

The list of the avifauna of the above mentioned localities showing the number of determined bones is as follows:

Węże I: *Tetrao conjugens* n. sp., 8; *Lyrurus* sp., 1; *Francolinus* (*Lambrechtia* n. sg.) *capeki wenzensis* n. ssp., 33; *Passeriformes* indet. 1.

Rębielice Królewskie I: *Aquila* (*Hieraetus*) sp., 1; *Lagopus lagopus atavus* n. ssp., 33; *Tetrao* aff. *praerogallus* Jánossy, 1; *Lyrurus* sp. — ? *Lagopus* sp., 3; *Francolinus* (*Lambrechtia*) *capeki vilányiensis* n. ssp. 240 (about 10—12 individuals); *Francolinus* (*Lambrechtia*) *minor* n. sp., 29; *Grus* (array of *G. grus*), 1; *Charadrius* (array of *Ch. morinellus*), 2; *Asio* aff. *flammeus* Pont., 1; *Glaucidium* sp., 1; *Strix* (array of *S. nebulosa*), 2; *Athene noctua veta* n. ssp., 1; *Bubo* sp., 1; *Sitta* sp., 1; *Turdus* sp., 8; *Luscinia* (array of *L. svecica*), 1; *Anthus* (array of *A. cervinus*), 1; *Aves* indet. (chiefly *Passeriformes*), 22;

Rębielice Królewskie II: *Francolinus* (*Lambrechtia*) *minor* n. sp., 6

Kadzielnia: *Glaucidium* sp., 1; *Francolinus* sp., 5

II. SYSTEMATIC DESCRIPTIONS

Order: *Falconiformes*

Family: *Accipitridae*

Subfamily: *Buteoninae*

Genus: *Aquila*

Aquila (*Hieraetus*) sp.
(see Plate XXIV. Phot. 2—3)

Material: Rębielice Królewskie I: phalanx II digiti 3 pedis.

The comparison of the phalanx with the corresponding bones in the genera *Falco* (larger species), *Pandion*, *Circaetus*, *Circus*, *Pernis*, *Milvus*, *Accipiter* (*gentilis*), *Buteo* (*buteo*, *lagopus*, *rufinus*), *Hieraetus* (*pennatus*, *fasciatus*) and *Aquila* sensu stricto (*clanga*) proves the close morphological resemblance with the two latter ones. The morphological similarity manifest itself chiefly in plantar and lateral view. Except for the small eagles, the buzzards show also similarity to the fossil bone, but the proportions are different in the latter one. The dimensions of the fossil as well as the comparative recent material are shown in Table I.

Table I

The measurements (in mm.) of the phalanx II digiti 3 pedis of a fossil eagle from Rębielice Królewskie I. in comparison with the sizes of recent birds of prey

Species		Length	Distal width
Aquila (*Hieraetus*) sp. fossil from Rębielice Królewskie		6·8	3·7
Recent birds:			
Buteo buteo	1.	8·0	3·8
	2.	7·7	3·6
	3.	7·2	3·4
Buteo lagopus	1.	6·4	4·1
	2.	7·0	4·0
Buteo ferox	1.	8·7	4·3
Hieraetus fasciatus	1.	13·4	6·2
Hieraetus pennatus	1.	8·2	4·2

Two facts emerge from this table: the fossil bone stands not only morphologically but also in the proportions nearest the Booted Eagle *H. pennatus* and it seems to be smaller than the minus-variants of this species. The wing length of my recent comparative specimen of the Booted Eagle was 385 mm.

If we assume the same proportions at the fossil form as at the recent one, the size of the phalanx suggests the wing length of 320 mm or less, considerable smaller than in the recent bird, wing length of which ranges between 350—430 mm. This calculation is of restricted use, because the allometrical differences might be only supposed. Many, mainly tropical forms of eagles in the Old World are known (*H. kieneri*, *ayresii*, *spilogaster*, *wahlbergi* etc.), considered by some authors as an array of species and the European Booted Eagle seems to be the smallest among them.

As mentioned above, the phalanx from Rębielice Królewskie is not convenient for drawing considerable conclusions, it suggests only with a high probability, that a tropical representative of birds of prey was a member of the ornithofauna of this locality.

Order: *Galliformes*

Family: *Tetraonidae*

Genus: *Lagopus*

Lagopus lagopus atavus n. ssp.
(see Plate XXIV. Phot. 4—8)

Material: Rębielice Królewskie I: oral fragments of two mandibles; coracoideum: 2 left and 3 right cranial ends, 2 right diaphyses; scapulae: 3 left cranial ends; humeri: 2 right proximal and 1 right distal fragments; radius: right distal end; ulnae: 1 left and 2 right proximal as well as 1 left and 1 right distal fragments; carpometacarpi: left and right entire specimens, 1 right proximal end; femur: left proximal end; tibiotarsus: right distal end; tarsometatarsi: 2 left distal ends; 1 phalanx I digiti 1 alae; 2 phalanges I digiti 2 alae; 1 phal. II dig. 2 pedis; 1 ulnare.

The most surprising in the whole fossil bird material from Poland is the presence of 33 bones of this small gallinaceous bird. The appurtenance of the remains to the family *Tetraonidae* is out of question. For detailed comparisons and for systematical identification the proximal end of the humerus is especially convenient. The form of the caput articulare, of the tricipital fossa as well as of the „eminentia" musculi latissimi dorsi posterioris (here a groove) are especially characteristic for *Tetraonidae*. Taking into account the size, *Lagopus lagopus* among Eurasian *Tetraonidae* might be supposed. American grouses of the genera *Centrocercus*, *Dendragapus*, *Tympanuchus*, *Canachites*, *Bonasa* and Asiatic *Falcipennis* have a morphologically similar humerus, but they have different proportions of this bone as shown in Table II.

The data of this table show not only the great conformity of measurements of the fossil bone with the recent *Lagopus* but also the robust form of all American grouses in opposition to the European smaller *Tetraonidae*. This latter fact

Table II

The measurements (in mm.) of the humerus of a fossil grouse from Rębielice Królewskie I on the background of recent smaller species of *Teiraonidae*

Species	Length	Proximal width	Width of diaphysis	Distal width
Lagopus lagopus atavus n. ssp. fossil from Rębielice Królewskie I.	—	16·0	6·0	—
Recent birds:				
Centrocercus urophasianus *	90·0	23·5	8·6	17·0
Dendragapus obscurus *	72·0	20·0	7·5	14·5
Tympanuchus cupido *	73·0	21·0	7·7	14·2
Canachites canadensis *	52·0	15·0	4·5	10·0
Bonasa umbellus	55·5	16·0	5·7	12·0
Tetrastes bonasia **	51·6	14·2	5·3	10·5
Lagopus mutus **	61·0	16·0	5·5	11·0
Lagopus lagopus **	60·0	16·5	6·0	11·7
Falcipennis falcipennis ***	58·0	—	6·0	—

* Measured on the specimens from the British Museum (N. H.) by courtesy of G. S. Cowles.
** Plus-variants.
*** Measured in the private collection of N. I. Burchak-Abramovich (Tbilisi) by courtesy of the owner.

proves clearly two different evolutionary lines of these gallinaceous birds existing on these two continents. In other bones differences are similar.

All other extremity bones from Rębielice show also specific characters on the background of the comparative material: there are some morphological differences in the proximal part of the humerus („eminentia" musculi latissimi dorsi posterioris is not an elevation but a groove and on the inner side of proximal epiphysis — in proximal view, there is a foramen, observed by me only in *Tympanuchus*), the distal end of the humerus seems to be slender, the phalanx I digiti 2 alae and the carpometacarpus are slightly thicker than the corresponding bones of my comparative osteological material (8 specimens of *Lagopus lagopus* and *mutus*).

To prove, that these differences are due not only to individual variation, I compared the distal width and the largest thickness (at the condylus radialis on the outer side of the bone) of a hundred specimens of humerus of *Lagopus* from the Upper Pleistocene (Würm) deposits of Hungarian localities (Peskö, Pilisszánto, Szelim, Jankovich-cave, Baits-cave, Bivak and Istállóskó-caves). On the scatter diagram showing the correlation of the above mentioned measurements of distal parts of the humeri of *Lagopus* from the Upper and Lower Pleistocene, a statistical difference can be proved (see fig. 1). The dimensions of the distal end of the humerus from Rębielice Królewskie are smaller than the same ones of hundred specimens of the Upper Pleistocene and recent ma-

terial. This fact proves systematic difference between the younger and older forms of the European Grouse. I propose therefore to apply the subspecific name *Lagopus lagopus atavus* n. ssp. for these finds.

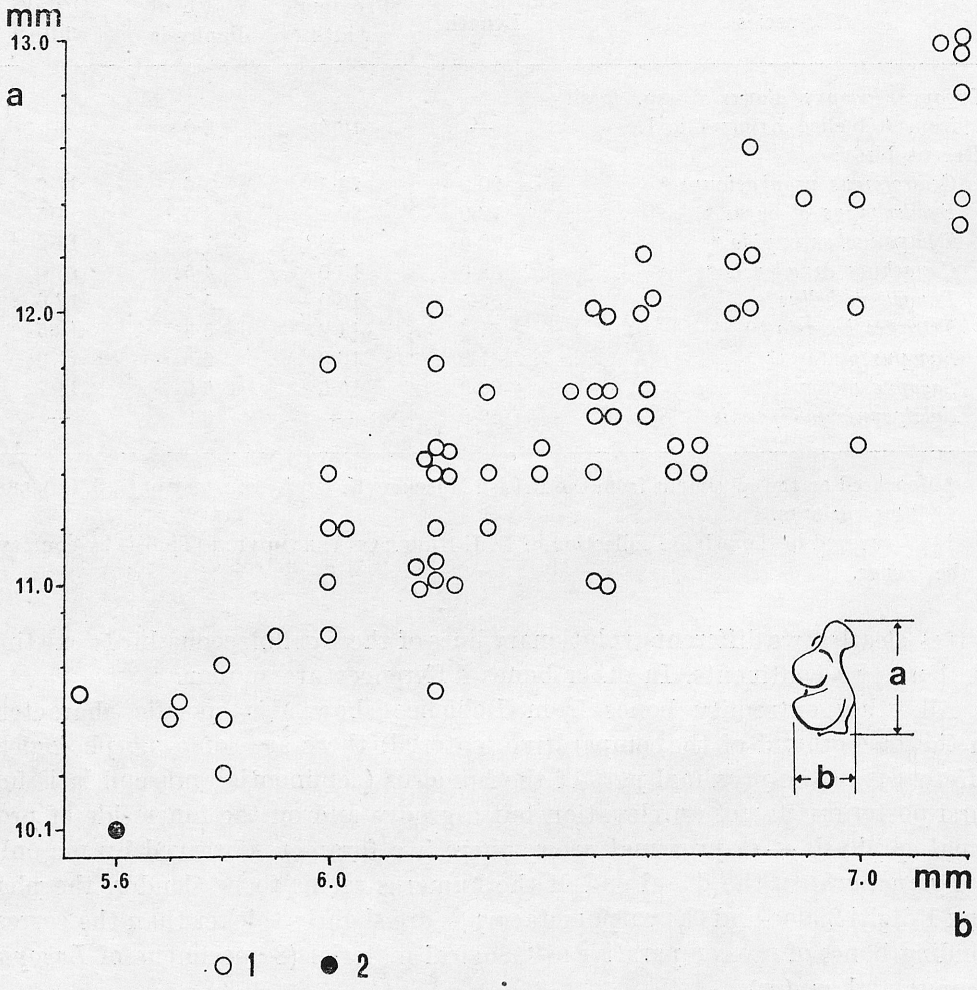


Fig. 1. The ratio of distal width and thickness of humerus of *Lagopus*: 1 — *Lagopus lagopus* and *L. mutus* (recent and from Upper Pleistocene), 2 — *Lagopus lagopus atavus* n. ssp. from Węże

We shall return to the ecological and climatological significances of this form of grouse. In any case we must point out, that the remains from Rębielice Królewskie are the first record of grouse in the Oldest Pleistocene („Villafranchian") of Europe. Recently it was possible to show the presence of *Lagopus* in Older Pleistocene at Stránská Skála, Vértesszölös and Koněprusy (Jánossy, 1970, 1972), but these localities are considerably younger than Rębielice Królewskie.

Genus: *Tetrao*

Tetrao conjugens n. sp.
(see Plate XXIII. Phot. 9)

Holotype: proximal fragment of the left carpometacarpus.

Referred specimens: ventral and dorsal fragments of left coracoideum (the same bone); distal end of left humerus; prox. end of left ulna; dist. end of left tarsometatarsus; dist. end of phalanx pedis.

Locus typicus et stratum typicum: Uppermost Pliocene („Lower Villafranchian"; Csarnotian) karst doline of the locality Węże I, Southern Poland.

Derivatio nominis: *conjugens*, from the latin word, conjugo — connect; due to the morphologically intermediate position *Tetrao* and *Lyrurus*.

Diagnosis: Middle sized species of *Tetraonidae* with a mosaic-like mixture of osteological features of *Tetrao urogallus* and *Lyrurus tetrix*.

Description: All bone fragments originate unambiguously from middle sized *Tetraonidae*. For the detailed analysis chiefly the distal end of the humerus and the proximal fragment of the carpometacarpus are adequate.

The fragmentary end of the humerus, according to its morphological features in lateral and distal views, stands close to corresponding bone of the hen of *Tetrao urogallus*. The measurements of the recent comparative material (partly according to EBERSDOBLER, 1968), as well as of the fossil piece are given in Table III.

Table III

Distal width of humerus and proximal width of carpometacarpus of *Tetrao conjugens* sp. n. from Węże compared with the measurements of bones of recent Capercaillies and Black Grouses

Species	Humerus		Carpometacarpus	
	No. of specimens	Distal width in mm.	No. of specimens	Proximal width in mm.
Tetrao conjugens sp. n. fossil from Węże		16·0		13·9
Recent birds:				
Tetrao urogallus ♂♂	37	21·0—26·0	30	20·0—22·6
Tetrao urogallus ♀♀	16	16·9—20·0	14	14·0—16·8
Lyrurus tetrix ♂♂	8	15·7—16·5	6	11·7—13·0
Lyrurus tetrix ♀♀	15	13·6—14·2	15	10·5—12·0

The largest thickness of the distal epiphysis ranges in the males of Capercaillie from 12·4 to 14·4 mm, in the females from 9·0 to 10·5 mm, in the Black Grouse (both sexes) 7·7—8·7 mm. In the fossil bone from Węże it measures 9·0 mm. So, the width indicates the plus-variant of Black Grouse and the thickness the minus-variant of Capercaillie.

A detailed analysis of the carpometacarpus proves a similar combination of features of the Capercaillie and the Black Grouse. The processus metacarpalis I. is more sharpened as in *Lyrurus*, the tuberositas metacarpalis II. (= muscularis) is nearer the proximal end of the bone as in *Tetrao*. The position of the foramen nutricium of the shaft is remarkable: it is considerably closer to the proximal end than in the specimens of the Black Grouse of the same size. I observed such a foramen in all metacarpi of the recent and Upper Pleistocene Black Grouse available, but I did not find it at recent or fossil Capercaillies. This fact indicates that the fossil carpometacarpus from Węże was in all probability shorter than the same bone of recent birds with the same proximal width. The intermediate metrical position of the correspondent bone of *Tetrao conjugens* is shown in Table III.

The distal end of the tarsometatarsus looks like the corresponding bone of the cock of the Black Grouse — the massivity of the distal part of the ulna gives the impression of a hen of *Lyrurus*. Eventually the fragments of the coracoid (from the same bone?) speak morphologically for *Lyrurus*, but allometrically for *Tetrao*.

Therefore the mosaic-like features alternating between *Lyrurus* and *Tetrao* show — in knowledge of this modus of evolution — the presence of an extinct form of *Tetraonidae* in the Upper Pliocene of Węże. This fact is significant because according to our present knowledge these are the oldest remains of true *Tetraonidae* in Europe.

Tetrao cf. *praeurogallus* JÁNOSSY 1969

Material: A phalanx II digiti 2 pedis from Rębielice Królewskie I falls in the variation of a hen of the Capercaillie, being relatively a little more slender (Table IV).

Table IV

The measurements (in mm.) of the phalanx II digiti 2 pedis of fossil *Tetrao* cf. *praeurogallus* from Rębielice Królewskie on the background of recent Capercaillies and Bl ck Grouses

Species	Length	Width of diaphysis
Tetrao cf. *praeurogallus* fossil from Rębielice Królewskie	15·7	3·0
Recent birds:		
Tetrao urogallus ♂	17·3	3·3
Tetrao urogallus ♀	15·0	2·8
Lyrurus tetrix ♂	12·8	2·4
Lyrurus tetrix ♀	11·0	2·2

Calculating the ratio of length and width of the phalanx, we find that with the size of the hen of *Tetrao* the slimness typical for *Lyrurus* (index: 2·0) can be observed. Due to this slimness I designate this form as *Tetrao* aff. *praeurogallus* JÁNOSSY, this species being characterized by slender extremity bones than in the recent species (JÁNOSSY, 1969).

Lyrurus sp. — ? *Lagopus* sp.

Material: Węże I: Distal end of right tibiotarsus
Rębielice Królewskie I: 2 phalanges I digiti 2 pedis,
phalanx I digiti 4 pedis.

Among the series of phalanges of *Francolinus* at Rębielice Królewskie I found three considerably larger than the other ones, having features of *Tetraonidae*. Both phalanges I digiti 2 are smaller and slimmer than the same bone in my recent comparative material (a minus variant of a hen of the Black Grouse). The proportions of the bones are fundamentally different from those in *Lagopus*.

Table V

The measurements (in mm.) of the phalanges digiti pedis of a fossil grouse from Rębielice Królewskie on the background of recent grouses

Bone	Species	Length	Width of diaphysis
Phalanx I digiti 2	*Lyrurus* sp. — ?*Lagopus* sp. fossil from Rębielice Królewskie		
	1	13·7	1·7
	2	12·0	1·7
	Recent birds:		
	Lyrurus tetrix ♀	14·4	1·9
	Lagopus lagopus (plus-variant)	10·0	1·8
Phalanx I digiti 4	*Lyrurus* sp. — ?*Lagopus* sp. fossil from Rębielice Królewskie	10·0	2·4
	Recent birds:		
	Lyrurus tetrix ♀	10·0	1·9
	Lagopus lagopus (plus-variant)	7·4	2·1

In contrast to this fact the proximal and distal parts of the mentioned phalanges show more features similar to *Lagopus* than to *Lyrurus*. Unfortunately the phalanges of the Lower Pleistocene Black Grouse are insufficiently known and therefore I suppose that among the remains found hitherto from this age there can be phalanges II digiti 2. Taking into account that we do not have comparative material from this anatomical unit of the extinct *Lyrurus*, it is impossible to decide whether the phalanges originate from *Lyrurus* or *Lagopus*. In the

latter case this would be the main argument for the taxonomical independence of the *Lagopus* of The Lowest Pleistocene.

Meanwhile no remains more complete, confirming this opinion could be found. I give the measurements of the fossil as well as the recent comparative material in Table V.

The width of the distal end of tibiotarsus from Węże measures 7·0 mm. The same measurement ranges in the recent material of *Lyrurus* (according to Ebersdobler, 1968) between 8·0—8·9 mm. However, the size and the morphological features are more like *Lagopus* than *Lyrurus*. The specimen is too fragmentary for further conclusions.

Family: *Phasianidae*

Genus: *Francolinus*

Subgenus: *Lambrechtia* n. sg.

Francolinus capeki wenzensis n. ssp.
Francolinus capeki villányiensis n. ssp.
(see Plate XXIII. Phot. 1—8)

Material: Rębielice Królewskie I: Fragment of premaxilla; fragm. of mandibula; 2 oral fragm. of sternum; coracoideum: 2 right ventral, 8 right and 6 left dorsal fragm.; scapula: 11 left and 1 right cranial fragm.; humerus: 1 complete left, 5 left and 4 right proximal, 10 left and 5 right distal fragm., 1 left and 1 right diaphysis; ulna: 2 left complete, 4 left and 4 right proximal, 3 left and 1 right distal fragm.; radius: right proximal, 5 left and 3 right distal fragm.; carpometacarpus: left complete, 4 left and 4 right proximal, 3 left and 4 right distal fragm.; femur: 1 left proximal, 1 left and 1 right distal fragm.; tibiotarsus: 1 right proximal, 7 left and 7 right distal fragm., 2 left and 1 right diaphysis, 1 juvenile distal fragm.; tarsometatarsus: right complete, 10 left and 4 right proximal, 7 left and 6 right distal fragm., 4 diaphysis; 1 ulnare; 12 phalanges I digiti 2 alae; 2 phal. II dig. 2 alae; 7 phal. I dig. 1 pedis; 9 phal. II dig. 2 pedis; 2 phal. II dig. 2 pedis; 3 phal. I dig. 3 pedis; 10 phal. I dig. 4 pedis; 18 phalanges unguis. About 10 phalanges of small *Galliformes* originate with high probability from the same species.

Material: Węże I: 2 fragments of premaxilla; coracoideum: left and right cranial frag.; humerus: 2 left and 2 right distal fragm.; radius: left prox. fragm.; ulna: 2 left prox. fragm. and left dist. fragm.; carpometacarpus: left and right prox. fragm.; femur: right proximal and two distal fragm.; tibiotarsus: left proximal and right distal fragm.; tarsometatarsus: 3 left prox., 3 left prox., 3 right and 2 left distal fragm. (one left is juvenile); 4 phalanges 1 digiti 2 alae.

The above listed remains of small *Galliformes* (more than 270 pieces of bones) justify a new detailed revision of this group.

It was Capek (1917) who mentioned as first the extinct forms of „*Perdix*"

from Püspökfürdö (= Betfia); LAMBRECHT (1933) recognized in it the genus *Francolinus* and described it as a new species *Francolinus capeki*. Besides the locality Püspökfürdö this form was known at that time also from Beremend (Southern Hungary) and Stránská Skála (Czechoslovakia). Later LAMBRECHT determined it (in: BRUNNER, 1933) from Sackdilling (S. Germany) too.

I revised lately the generic determination of the fossil bones. I had the chance to compare the remains with the skeletons of following *Perdicinae* species: *Margaroperdix madagascarensis*, *Perdicula asiatica*, *Synoicus australis*, *Rollulus roulroul*, *Bambusicola thoracica*, *Caloperdix aculae*, *Lerva lerva*, *Ammoperdix heyi* and *griseogularis*, *Tetraogallus altaicus*, *Arboricola javanica*, *Alectoris graeca*, *Perdix perdix* and *P. daurica*.

Although there are some resemblances with certain other genera (e. g. the humerus is reminiscent of those of *Rollulus*, *Ammoperdix* or *Arboricola*, the tarsometatarsus — of *Synoicus*) the morphological relations seem to be closest with *Francolinus*.

The species of the genus *Francolinus* are today widespread in Southern Asia and Africa, formerly they occurred also in Southern Europe. The genus has been divided preciously into about 50 species; according to recent revisions about 30—33 species are valid (see chiefly HALL, 1963). During the last years I revised the skin and skeleton material of the phenotypical very homogeneous francolin-group in larger European museums (chiefly in the British Museum Natural History and in the Museum in Berlin). I give here the list of all species hitherto known, according to the different size groups, to make it possible to compare them with the fossil taxa (Table VI).

There exist complete skeletons of only a few species of *Francolinus* in different museums of Europe, but in spite of this I had the possibility to measure the length of the extremity bones of different forms of all the three size categories. These measurements compared with the corresponding ones of the fossil bones of *Francolinus capeki* are presented in Table VII.

A detailed osteological analysis gave following results: the recent genus is osteologically not homogeneous, there are some very aberrant forms e. g. *Francolinus jacksoni* or *F. bicalcaratus*, with fundamentally different osteological features than in other Francolins.

The fossil material comes in all osteological features close to the smaller and middle group of Francolins, but there are clear differences too. We cannot identify it neither morphologically nor allometrically with any of the recent species. In all features the nearest one — among the examined recent species — is the forest Francolin *F. lathami* from Africa (a convergence?), but in this case also there are osteological differences, and this species has a long and spiked premaxilla in opposition to the fossil form. The former European species *Francolinus francolinus*, stands morphologically and metrically far from our fossil form. None of the recent forms has such a deep tricipital fossa on the humerus as the fossil one. Moreover all cocks of the examined recent species have on the tarsometatarsus one or two spurs (diagnostic feature of the genus),

The comparison of the length (in mm.) of the wing and tarsus of the recent representatives of the genus *Francolinus*

Species	Length of wing	Length of tarsus
1. "Small" species		
Africa:		
Francolinus coqui (SMITH, 1836)	125—147	36—40
Francolinus schlegeli HEUGLIN, 1863	121—137	33—36
Francolinus hartlaubi BOCAGE, 1869	130—150	37—43
Francolinus albogularis HARTLAUB, 1854	128—143	38—40
Francolinus sephaena (SMITH, 1836)	130—162	42—48
Francolinus lathami (HARTLAUB, 1854)	147—149	41
Francolinus nahani DUBOIS, 1905	142—147	35—38
Asia:		
Francolinus pintadeanus (SCOPOLI, 1786)	—	39
Francolinus pondicerianus GMELIN, 1789	140—152	44
2. "Middle-sized" species		
Africa:		
Francolinus shelley O. GRANT, 1890	155—179	38—45
Francolinus levaillanti (VALENCIENNES, 1925)	159—180	47—54
Francolinus harwoodi BLUNDELL and LOVAT, 1899	180—190	52
Francolinus finschi BOCAGE, 1881	165	40
Francolinus adspersus WATERHOUSE, 1838	160—190	47—54
Francolinus natalensis A. SMITH, 1834	160—180	43—52
Francolinus bicalcaratus LINNAEUS, 1766	155—170	52—58
Francolinus icterorhynchus HEUGLIN, 1863	163—169	48—58
Francolinus clappertoni CHILDREN, 1826	167—200	50—55
Francolinus swierstrai (ROBERTS, 1929)	180	52
Francolinus hildebranti CABANIS, 1878	155—195	45—55
Francolinus squamatus CASSIN, 1857	160—190	50—52
Francolinus shatensis TEMMINCK, 1851	167—192	55—60
Francolinus griseo-striatus O. GRANT, 1890	150—160	50
Francolinus camerunensis ALEXANDER, 1909	168—181	55—60
Francolinus nobilis REICHENOW, 1908	188—203	55
Francolinus africanus STEPHENS, 1819	170—180	40—45
Asia:		
Francolinus francolinus LINNAEUS, 1766	170—180	47—57
Francolinus pictus (JARDINE and SELBY, 1828)	—	46
Francolinus gularis (TEMMINCK, 1815)	180	57
3. "Large" species *		
Africa (only):		
Francolinus castaneicollis SALVADORI, 1888	176—230	63—65
Francolinus capensis (GMELIN, 1789)	190—230	67
Francolinus ochropectus DORST and JOUANIN, 1952	212	63
Francolinus jacksoni O. GRANT, 1891	205—247	73
Francolinus erckellii (RÜPPEL, 1835)	191—232	45—60

* Barethroated Francolins or "spurfowls", members of the genus *Pternistes*, are not included in this table because they all belong to the largest category, not represented in the fossil material by now.

Table VII

The lengths of different extremity bones (in mm.) of the fossil *Francolinus capeki* and some recent members of the genus *Francolinus*

Species	Coracoideum	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
Francolinus capeki fossil							
1. from Betfia (Püspökfürdö)	36	42	42	23	—	—	38
2. from Koněprusy	—	43	40	24	—	—	36
3. from Rębielice Królewskie	—	42	40	24	—	—	39
Recent birds:							
1. Small species:							
Francolinus pondicerianus	31	44	40	24	46	63	44
Francolinus pintadeanus	34	46	41	24	53	60	39
Francolinus sephaena	32	46	42	25	49	66	42
Francolinus coqui	30	45	43	24	45	57	36
Francolinus lathami	33	43	43	23	45	61	41
2. Middle-sized species:							
Francolinus clappertoni	40	52	48	28	55	73	50
Francolinus bicalcaratus	42	56	52	29	67	80	56
Francolinus pictus	35	50	43	27	55	67	46
Francolinus francolinus	36	55	49	29	58	72	47
Francolinus levaillantii	41	52	48	28	60	75	54
Francolinus gularis	37	56	51	28	60	85	57
3. Large species:							
Francolinus jacksoni	51	72	68	37	86	110	73
Francolinus capensis	51	69	64	37	76	100	67

entirely lacking in the fossil forms. As we shall see later, the phalanges of the Francolin from Rębielice Królewskie are allometrically quite different from the recent ones.

Considering all these facts I propose to separate the fossil Francolins from the recent ones, as a distinct subgenus, under the name *Lambrechtia*, in the honor of Coloman LAMBRECHT, the Hungarian paleoornithologist.

The detailed description of the larger Francolin remains of the Upper Pliocene-Lower Pleistocene of Poland is as follows. The humerus is convenient for a detailed analysis. Table VIII shows the measurements of this bone from the fossil material from different geological ages.

Besides the measurements given in table VIII, some smaller series of the same data, measured (in mm) on fragments from Rębielice Królewskie I are as follows:

proximal width: 11·0; 11·4; 11·7;

distal width: 7·7; 8·0 (2×); 8·1; 8·2 (2×); 8·3; 8·4 (2×); 8·5; 8·6;

width of diaphysis near the middle of the bone: 3·8; 4·0 (2×); 4·1 (3×); 4·2;

The distal width of the fragments of humeri from Węże has following measurements: ±7·0; 7·8 (3×). At Osztramos 8 (new, unpublished locality from Northern Hungary of the same age as Osztramos 2): 8·2 mm.

Table VIII

The measurements (in mm.) of humeri of *Francolinus capeki* from different localities, compared with recent *Francolinus coqui*

Specimen	Total length	Proximal width	Distal width	Width of the diaphysis at the middle of the bone
Francolinus capeki, fossil:				
from Betfia (Püspökfürdö) — type specimen	42·7	12·0	8·3	4·6
from Betfia (Püspökfürdö)	—	11·7	—	4·3
from Betfia (Püspökfürdö)	—	—	8·4	—
from Stránská Skála	43·4	11·8	8·6	4·2
from Koněprusy	43·0	11·7	8·6	4·4
from Beremend	40·0	10·8	±7·0	3·8
from Rębielice Królewskie	42·1	11·0	7·8	4·1
from Rębielice Królewskie	±40·0	11·4	—	4·3
Francolinus coqui, recent	45·3	11·2	8·2	3·7

Although present material is unfortunately not convenient for statistical investigations, the tendency of the geologically older bones of Francolins being slimmer can be observed. It can be seen chiefly in the width of the diaphysis, which in the material from Betfia, Stránská Skála and Koněprusy (all of similar geological age) ranges between 4·2—4·6 mm (n = 4), what is the variation-range of the same measurements from Beremend and Rębielice Królewskie being 3·8—4·2 mm (n = 8). There seem to exist also some other morphological differences, chiefly in the proximal epiphysis of the humeri, but these are not distinctive. So the caput articulare seems to be higher and the tricipital fossa lower, as well as the crista lateralis (pectoralis) in average broader in the geologically younger form.

The length of two complete ulnae from Rębielice Królewskie I is 39·5 and 40·0 mm, the width of the diaphysis (both pieces measured when lying on a flat surface) 3·0 mm.

The measurements of carpometacarpus from the different localities are given in Table IX. The proximal width of further specimens of this bone from Rębielice Królewskie I. measures: 6·3; 6·6 (2×); 6·8; 7·0; 7·3 mm. The same measurement in the francolin-material from Węże is as follows: 6·0; 6·2; 6·3; 6·7 mm.

Table IX

The measurements (in mm.) of the carpometacarpus of *Francolinus capeki* from different localities

Locality	Length	Proximal width	Distal width	Width of the diaphysis at the middle of the shaft
Betfia (Püspökfürdö)	23·3	6·6	4·8	2·3
Koněprusy	24·0	6·7	4·0	2·2
Rębielice Królewskie I.	23·9	6·8	4·2	2·3

Table X

The measurements (in mm.) of the tarsometatarsus of *Francolinus capeki* from different localities

Locality		Total length	Proximal width	Distal width	Width of the diaphysis at the middle of the bone
Betfia (Püspökfürdö)	1.	37·6	5·8	7·0	4·2
	2.	38·0	6·7	7·4	4·2
Koněprusy		±36·0	—	7·2	3·0
Rębielice Królewskie I.		39.2	6.6	7.0	3.0

The distal width of femur from Rębielice Królewskie I. measures 7·5 mm, the same from Węże 6·6 mm.

The distal ends of tibiotarsi measure in the material from Rębielice Królewskie: 5·6; 5·8 (2 ×); 5·9; 6·0 (4 ×); 6·2 (2 ×); 6·3; 6·4mm. The same measurement in the unique specimen from Betfia (Püspökfürdö) is 6·0 mm, from Stránská Skála 6·8 mm; from Węże 5·5 mm, from Villány-Nagyharsányhegy 6·5 mm.

The measurements of the tarsometatarsi are shown in Table X. The distal widths of further specimens from Rębielice Królewskie are: 7·2; 7·3; 7·4; 7·6 mm; from Betfia 7·0; 7·2; 7·5 mm; from Węże: 6·0; 6·7; 7·2 mm; from Osztramos 2 (a new unpublished locality in Northern Hungary of the age of Betfia) 7·2 mm.

As mentioned above — none of the tarsometatarsal bones has any traces of a spur.

The measurements of the phalanges of the foot of *Francolinus capeki* compared with these of recent *F. francolinus* and *F. coqui* are given in table XI.

These measurements show fundamental allometrical differences between the phalanges of the true Francolin and of the fossil form. Unfortunately phalanges were not collected up to now from localities geologically younger than Rębielice Królewskie (e. g. Betfia etc.).

Table XI

The measurements (in mm.) of the phalanges digiti pedis of the fossil *Francolinus capeki* from Rębielice Królewskie compared with recent *Francolinus coqui* and *F. francolinus*

Specimen	Phalanx I digiti 1		Phalanx I digiti 2		Phalanx II digiti 2		Phalanx I digiti 3		Phalanx I digiti 4	
	Length	Width of diaphysis	Length	Width of diaphysis	Length	Width of diaphysis	Length	Width of diaphysis	Length	Width of diaphysis
Francolinus capeki, fossil from Rębielice Królewskie										
1	10·2	1·2	13·4	1·4	11·0	1·3	10·3	1·8	9·8	1·5
2	9·2	1·2	13·4	1·4	10·7	1·2	10·2	1·8	9·2	1·5
3	9·2	1·1	13·6	1·5	—	—	—	—	9·9	1·4
4	9·0	1·1	13·3	1·5	—	—	—	—	9·9	1·5
5	9·3	1·0	13·5	1·3	—	—	—	—	7·7	1·3
6	8·9	1·2	13·5	1·4	—	—	—	—	9·8	1·5
7	—	—	12·9	1·3	—	—	—	—	9·5	1·5
8	—	—	13·0	1·3	—	—	—	—	9·5	1·5
Recent birds:										
Francolinus coqui	5·0	1·2	7·8	1·4	6·0	1·3	9·4	1·8	6·1	1·4
Francolinus francolinus	6·2	1·5	11·4	1·7	8·3	1·6	13·1	2·3	8·4	1·9

A detailed comparison between the phalanges II digiti 2 alae of the *Francolinus capeki* from Węże and Rębielice Królewskie shows no differences. To make further comparisons easier in the future I give the measurements of these bones in table XII.

At last we have to mention the morphological features of the premaxillae. One of these bones is present in Rębielice Królewskie and two specimens in Węże. At first sight it appears that the premaxillae from Węże are considerably larger than the same bones from Rębielice Królewskie. This fact is all the more remarkable, because — as mentioned above — nearly all bones of this bird are smaller at Węże than at Rębielice Królewskie. Consequently, the premaxillae seem to variate in the opposite direction than the limb bones, what speaks for an allometric difference between these two forms. On the other hand there can be seen on this bone in proximal view two apertures as in the recent Francolins. The wall separating these apertures is considerably more massive in the material from Węże as well as in the specimen from Rębielice Królewskie. There-

fore I exclude the possibility of sexual dimorphism. This fact becomes another reason for separating the „cotypes" of *Francolinus capeki* and the geologically older forms. The premaxilla varies considerably in the different recent species of Francolins, but in most cases it is longer and spiker than in the fossil ones.

Table XII

The measurements (in mm.) of the phalanx II digiti 2 alae of *Francolinus capeki* from Rębielice Królewskie I. and from Węże

Locality/Specimen No.		Length	The largest width
Rębielice Królewskie I.:	1	9·5	4·3
	2	9·5	4·3
	3	9·5	4·5
	4	9·6	4·3
	5	9·7	4·3
	6	9·7	4·4
	7	±10·0	4·3
	8	10·0	4·3
	9	10·0	4·7
	10	10·1	4·7
Węże	1	10·0	4·5
	2	10·3	4·3

Due to the above mentioned metrical and morphological differences (i. e. differences in the range of the measurements of different extremity bones, with greater or smaller overlappings, on the one hand, and the differences of the praemaxillae on the other) I propose for these stratigraphically different forms the following subspecific names:

Francolinus capeki wenzensis s. ssp. for the form from Węże and

Francolinus capeki villanyiensis n. ssp. for the form from Rębielice Królewskie, Beremend, Osztramos 7 and Villany-Kalkberg,

Francolinus capeki capeki for the form from Betfia, Koněprusy, Sackdilling, Stránská Skála and Osztramos 2 and 8.

Francolinus (*Lambrechtia*) *minor* n. sp.

Holotype: left, nearly intact carpometacarpus from Rębielice Królewskie I.

Locus typicus et stratum typicum: „Middle Villafranchian", („Villanyian") fissures in Rębielice Królewskie I. in Southern Poland.

Derivatio nominis: minor, due to the small dimensions.

Diagnosis: Small species of Francolin, smaller from the hitherto known recent or fossil forms with the morphological features of the present known fossil European francolins (subgenus *Lambrechtia*).

Material: Rębielice Królewskie I: coracoideum: 2 left and 1 right cranial, 1 left ventral and 1 right diaphysis fragments; scapulae: left and right cranial ends; humeri: 2 left proximal and 3 left distal ends; ulna: right proximal end; radii: 2 right distal ends; carpometacarpi: left and right entire specimens, left proximal and right diaphysis fragm.; femur: right distal end; tibiotarsi: left proximal and distal ends; tarsometatarsi: right proximal, right and two left distal ends; 2 phalanges I digiti 2 alae; phalanx I digiti 1 alae; phalanx I digiti 2 pedis.

Material: Rębielice Królewskie II: ulna: right distal end; radii: 2 proximal ends; carpometacarpi: left and right proximal and right distal ends; tibiotarsus: right distal end.

Table XIII

The comparison of the measurements (in mm.) of different bones of the fossil *Francolinus minor* sp. n. and *Fr. capeki*

Bone and measurement	*Francolinus minor* sp. n.		*Francolinus capeki*	
	Size	No. of specimens	Size	No. of specimens
Carpometacarpus:				
length	20·1—21·2	2	23·3—24·0	3
proximal width	5·7—6·0	6	6·0—7·3	13
Humerus:				
distal width	6·7—6·9	3	7·0—8·6	20
width of diaphysis	3·2—3·4	2	3·7—4·6	15
Tarsometatarsus:				
distal width	5·0	1	6·0—7·6	15
width of diaphysis	2·2—2·5	2	3·0—4·2	15
Tibiotarsus:				
distal width	4·9	1	5·5—6·8	16
Femur:				
distal width	5·2	1	6·6—7·5	2
Phalanx I digiti 2 alae:				
length	9·1	1	9·5—10·3	12
width	3·7	1	4·3—4·7	12
Phalanx I digiti 2 pedis:				
length	7·8	1	10·2—10·3	2
width of diaphysis	1·0	1	1·8	2

Description: Studied bones of the species are morphologically nearly identical with the corresponding ones of *Francolinus capeki*, they belong therefore clearly to the subgenus *Lambrechtia*. The form of the carpometacarpus and the tarsometatarsus supports this statement. The special torsion of the trochlea digiti 4 of the latter bone speaks especially clearly for this subgenus.

The size not only falls below the variation of the known fossil form of Francolins, but underneath the measurements of recent forms which I have measured as well.

Measurements of fossil species in comparison with the variation ranges of the corresponding bones of the different subspecies of *Francolinus capeki* as well as the numbers of specimens known up to now are given in Table XIII.

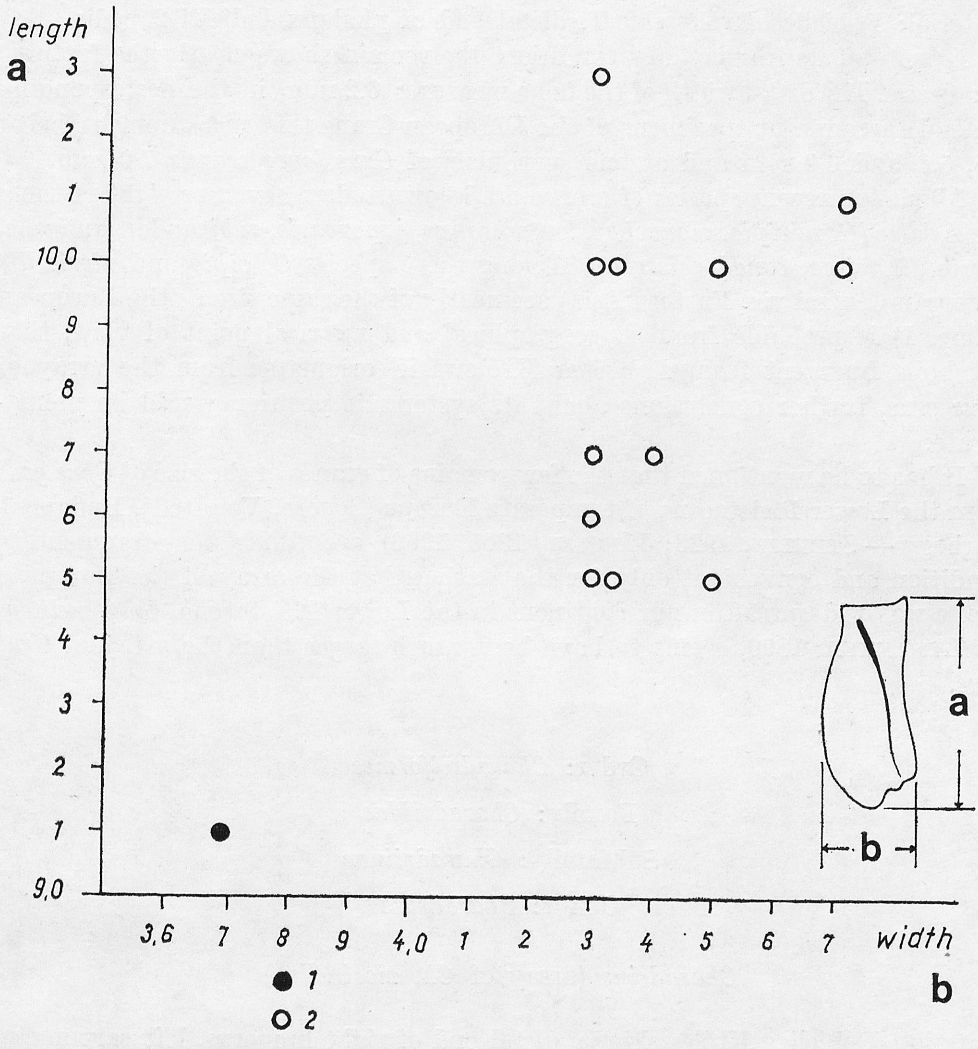


Fig. 2. The ratio of length and width of the phalanx I digiti 2 alae of *Francolinus minor* n. sp. (1) and *Francolinus capeki* (2)

Table XIII points out not only to the difference in size of nearly all extremity bones between this form and *Francolinus capeki*, the only known fossil species of this genus, but (in the phalanges, chiefly in phalanx I digiti 2 alae) to a distinct allometrical difference as well. This fact emphasizes the taconomical independence of this form (see fig. 2).

Order: *Gruiformes*

Family: *Gruidae*

Genus: *Grus*

Grus (array of *G. grus*)

Material: Rębielice Królewskie I: distal end of phalanx I digiti 2 pedis.

Despite of its fragmentary condition, the remain shows clearly the features of a Crane. The distal width of the bone measures 6.2 mm, in the corresponding bone of three recent specimens of the European Crane this measurement being 5·5, 5.8 and 6·0 mm and at one specimens of *Grus leucogeranus* 7·0 mm.

About ten recent species of cranes are known today, seven or eight of them are Asiatic (*Grus vipio*, *monachus*, *leucogeranus*, *japonensis*, *rubicundus*, *antigone*, *nigricollis*, *virgo*, *canadensis* etc.). Among these species *G. vipio* and *nigricollis* (living in Central viz. Eastern Asia) are nearly of the same size as the European Crane. It is probable from zoogeographical and metrical point of view, that the bone fragment from Rębielice Królewskie originates from the array of *Grus grus*, further conclusions about its systematic position would be prematurate.

It has to be mentioned that the few remains of cranes of the size of *Grus grus* from the Lower Pleistocene of temperate Europe (Senèze, Voigstedt, Budapest-Várhegy — Stehlin, 1923; Jánossy, 1965 1969) are also in very fragmentary condition and convenient only for the stating that the array of the European Crane was widespread in our continent in the Lower Pleistocene. *Grus melitensis* Lydekker 1890, seems to have been much larger than the array of *Grus grus*.

Order: *Charadriiformes*

Family: *Charadriidae*

Subfamily: *Charadriinae*

Genus: *Charadrius*

Charadrius (array of *Ch. morinellus*)

Material: Rębielice Królewskie I: distal end of right humerus, left carpometacarpus without metacarpale III.

A detailed comparison of the bones with different members of practically all European genera of plovers and allies (*Charadrius*, *Calidris*, *Squatarola*, *Limicola*, *Tringa*, *Philomachus*, *Limosa*, *Vanellus*, *Hoplopterus*, *Numenius*, *Glareola*, *Scolopax*, *Phalaropus*, *Crocethia*, *Burhinus*, *Recurvirostra*, *Himantopus*, *Arenaria*, *Haematopus*, *Capella*, *Lymnocryptes*) proves a very close relation to the genus *Charadrius* (sensu stricto).

The shape of the trochlea carpalis (incisura externa fide BALLMANN, 1969a), the fossa carpalis interna and the processus metacarpalis I of the carpometacarpus, as well as the shape of the impressio musculi brachialis inferioris and the epicondylus medialis of the distal part of humerus are equally characteristic for the plovers.

Table XIV

The measurements (in mm.) of the carpometacarpus of the fossil plover from Rębielice Królewskie I. compared with those of recent European plovers of similar size

Species	Length	Width of diaphysis	Proximal width
Charadrius sp., fossil, from Rębielice Królewskie I.	30·0	2·0	7·4
Recent birds:			
Charadrius morinellus	26·6	2·2	6·5
Charadrius apricarius	32·3	3·0	8·0

The measurements of carpometacarpus only are given in Table XIV. They show clearly, that the fossil bone is slightly longer and slender than that of *Ch. morinellus* but does not reach the dimensions of *Ch. apricarius*, chiefly in robustness (the wing length of my recent comparative material of *Ch. apricarius* was 173 mm, and it is therefore a minus variant: position in the variation range of my specimen of *Ch. morinellus* is unknown). No species in the size between *Ch. morinellus* and *Ch. apricarius* is known in Europe, and there is no hope for any comparison with recent forms of other continents which are osteologically unknown. Depending on the generic delimitation there are known 30—40 species of plovers in the Old and New World: some of them fall in the same size category as our fossil remains (e. g. *Charadrius asiaticus*, *vociferus* or *montana* etc.).

Therefore, we can state only, that in Plio-Pleistocene times there was in Europe a plover very similar to the recent European Dotterel.

Order: *Strigiformes*

Family: *Strigidae*

Genus: *Asio*

Asio aff. *flammeus* (PONTOPPIDAN 1763)

Material: Rębielice Królewskie I: phalanx I digiti 2 pedis.

A detailed comparison of the phalanx with the same bone of different owls proved very close morphological relation with the genus *Asio*. The same phalanges of other genera of European owls (*Strix*, *Nyctea*, *Bubo*, *Athene*, *Otus*,

Glaucidium, Surnia) are metrically or morphologically considerably different. Within the genus *Asio* the bone, with its heavier form, stands closer to *Asio flammeus* than to *Asio otus*, as is shown in Table XV.

As can be seen from this table the morphological and metrical similarity with the Short-eared Owl *A. flammeus* is unambiguous. It is, however, impossible to decide on the basis of a phalanx if there are differences — if any — between the recent species and the fossil one.

Table XV

The measurements (in mm.) of the phalanx I digiti 2 pedis of the fossil owl from Rębielice Królewskie 1., compared with the measurements of the bones of recent European members of the genus *Asio*

Species	Length	Proximal width	Distal width
Asio aff. *flammeus*, fossil from Rębielice Królewskie I.	8·3	5·3	3·6
Recent birds:			
Asio flammeus			
1	8·4	5·5	3·5
2	8·2	5·6	3·7
3	8·4	5·6	3·6
4	8·6	5·4	3·7
Asio otus			
1	8·4	5·1	3·0
2	7·9	4·8	3·2
3	8·3	4·6	3·2
4	8·2	4·6	3·0
5	7·8	4·6	3·0
6	8·6	4·6	3·0

It is in any case remarkable, that the Short-eared Owl was here found together with *Lagopus*, as well as in the „cold" period of Middle Pleistocene („Mindel" of Stránská Skála and Vértesszöllös, Jánossy, 1970, 1972) and in many Upper Pleistocene localities of Europe. Nevertheless, we must be careful as to the climatological conclusions, drawn from this fact because this species is cosmopolitic today and breeds also in South Africa and South America.

Genus: *Glaucidium*

Glaucidium sp.

Material: Rębielice Królewskie I: distal end of phalanx III. digiti 3 pedis.
Material: Kadzielnia: right tarsometatarsus, proximal and distal ends broken.

Comparing the phalanx fragment with the corresponding bones of *Aegolius*, *Athene*, *Otus* and *Glaucidium* (of nearly the same size), we see that the propor-

tions, dimensions and the morphology (chiefly the special form of cavity before the distal end) speak with great probability for the presence of the genus *Glaucidium* in our localities (I have for comparison only the corresponding phalanx of *Glaucidium brasilianum* and not of *G. passerinum*). This piece is, of course, not convenient for further conclusions. Even the proper generic place is not certain.

Table XVI

The measurements (in mm.) of the tarsometatarsus of Pygmy Owl from Kadzielnia compared with the fossil and recent specimens of *Glaudicium passerinum*

Specimen	Length	Proximal width	Distal width	The smallest width of diaphysis
Glaucidium sp., fossil				
from Kadzielnia	—	—	±5·0	2·8
Glaucidium passerinum, fossil				
from Stránská Skála	17·0	5·4	5·3	3·3
from Hundsheim	16·4	±4·8	5·0	2·7
from Żytnia Skała *	17·4	5·6	±6·0	—
Glaucidium passerinum, recent coll. Capek, Brno **				
1	17·7	—	5·4	—
2	17·7	—	5·4	—
coll. Budapest	18·0	5·3	—	2·3
acc. Nehring	17·0	5·6	5·0	3·0

* Collection of the Institute of Systematic and Experimental Zoology Pol. Ac. Sc., Kraków.
** Measured by Z. Bocheński, Kraków.

The fragment of tarsometatarsus, however, proves unambiguously the presence of the Pygmy Owl in the Lowest Pleistocene of Poland. The taxonomical relations of *Glaucidium* of Lower-Middle Pleistocene and of Upper Pleistocene viz. recent are not clear, due to the small number of fossil remains. To make further comparisons easier the measurements of the tarsometatarsi of Pygmy Owls, just now available to me, are given in Table XVI.

The measurements in Table XVI show that the Lower Pleistocene Pygmy Owls are in close relation with the Eurasian recent species, considered by zoologists as a clear taiga-alpine element. A relation with South Asiatic, African and American species — usually with other dimensions — is not probable.

Genus: *Strix*

Strix sp. (array of *S. nebulosa*)

Material: Rębielice Królewskie I: lateral fragment of the distal end of right tarsometatarsus; distal end of phalanx II digiti 3 pedis.

Notwithstanding the very fragmental condition of both pieces the features

of owls can unambiguously be recognized on these pieces. Especially the distal fragment of the phalanx seems to be very characteristic for the genus *Strix* (sensu stricto). A little groove behind the distal epiphysis on the upper (plantar) side of the bone suggests the presence of this genus in opposition to *Bubo*, *Nyctea*, *Asio*, *Surnia* from the nearer size category — not speaking about *Tyto* with quite different morphological features. The form of the shaft of the fragment of phalanx (its slimness) is similar to the Ural Owl *Strix uralensis*, the extension of the distal epiphysis approaches it to *Strix nebulosa* (see Table XVII).

Table XVII

The measurements (in mm.) of the fragment of the phalanx II. digiti 3 pedis of the fossil *Strix* sp. from Rębielice Królewskie I., compared with recent members of genus *Strix* in Europe

Species	Width of diaphysis	Distal width
Strix sp., fossil from Rębielice Królewskie I.	3·8	5·5
Recent birds:		
Strix nebulosa	4·0	5·4
Strix uralensis	4·0	5·0
Strix aluco (plus-variant)	3·2	4·2

The fragment of tarsometatarsus is adequate only to state that this bone and above mentioned phalanx belonged to the owl of nearly the same size.

These remains are sufficient only for the conclusion, that an owl of the size of *Strix nebulosa* was living during the times of the deposition of Rębielice Królewskie. It is remarkable that very fragmentary remains of an owl of nearly the same size as our present findings were determined from the geologically considerably younger Stránská Skála (Jánossy, 1972,- see also Skutil, Stehlik, 1939).

Genus: *Bubo*

? *Bubo* sp.

Material: Rębielice Królewskie I: distal broken? phalanx II digiti 2 pedis.

The fragment of a phalanx proves unambiguously the presence of a great owl, nearly of the size of the Eagle-Owl *Bubo bubo*. A detailed comparison of the remain with the corresponding phalanx (phalanx II digiti 2) of the larger owls of Europe suggested also the close morphological resemblance with *Bubo*. The proximal width of the bone measures 6·0 mm, at the smallest specimen of my recent comparative material of *Bubo* (a male) 7·6 mm. However, it is

a remarkable fact, that a foramen nutricium on the lower surface (volar view) of the distal part of this damaged phalanx can be seen. The position and form of the foramen point for *Bubo*, but the distance of this element from the proximal end of the corresponding phalanx of the Eagle Owl is considerably longer than in the fossil piece. This distance measures in the above mentioned male specimen of *Bubo* (with the proximal width of 7·6 mm) 16·4 mm, at the fossil specimen (with the proximal width of 6·0 mm) 10·9 mm. Therefore the fossil animal must have had a considerably shorter and broader phalanx than the recent European Eagle Owl.

It is clear, that even the generic position of the fragment is uncertain.

Genus: *Athene*

Athene noctua veta n. ssp.
(see Plate XXIV. Phot. 1)

Material: Rębielice Królewskie I: proximal part of left coracoideum.

A detailed comparison of the fossil bone with the corresponding ones of the recent European forms of the same size category, as *Glaucidium*, *Aegolius*, *Athene* and *Otus* proves a very close resemblance with the Little Owl *Athene noctua*. The form of the acrocoracoid, of the groove between the procoracoid and the shaft of the bone, as well as the facies (or fossa) glenoidalis and scapularis speak unambiguously for the belonging to the genus *Athene*. I have for comparison 13 specimens of the Little Owl so that the morphological variation of the bone can be stated. One can observe, that the position and depth of the foramen pneumaticus (below the acrocoracoid) are very variable, but it is never so reduced in the recent specimens as in the fossil one. Especially characteristic for the fossil form is the shape and size of the fonestra coracoidea (following Lambrecht (1933); in Ballmann (1969a): „foramen supracondyloideum"; in Ballmann (1969b) erroneously „foramen pneumaticum"). This foramen is evidently smaller than in all recent specimens. The measurements of this element of the fossil specimen are 0·7×0·4 mm, in the smallest recent bone 1·1×0·6 mm, in the largest one 2·0×0·9 mm.

Due to these slight but visible constant differences I propose to use for this form the subspecific name *Athene noctua veta* n. ssp.

According to the conception in the recent literature the array of *Athene noctua* is one taxonomical unit except for South Asiatic species *Athene brama* Temminck and *A. blewitti* (Hume), not differing in size from the typus generis, but only in the colour of plumage. So a comparison of the fossil form with the recent ones is of no reason for.

It has to be mentioned, that the Little Owl was uncommon in the Upper Pleistocene of Europe (Lambrecht, 1933, and Brodkorb, 1971: 7 records, partially stratigraphically uncertain).

I had the possibility to study the only remain of this owl from the Lower-

Middle Pleistocene of Europe (a phalanx III digiti 4 from Betfia (= Püspökfürdö) described by Capek, 1917), which seems to originate not from an owl but rather from a diurnal bird of prey (? *Circus* sp.). The determination is in any case uncertain. The remain from Rębielice Królewskie is therefore the first sure record of *Athene* from the Villafranchian of Europe.

Order: *Passeriformes*

As it is well known, the Song Birds are osteologically very homogeneous and therefore difficult to determine specifically. This is especially true for Lower Pleistocene and older remains, which must be compared not only with European forms but also with species of other continents. Inspite of these difficulties I tried to determine some bones of Song Birds from Rębielice Królewskie, although a part of them must have remained undetermined.

Suborder: *Passeres*

Family: *Sittidae*

Subfamily: *Sittinae*

Genus: *Sitta*

Sitta sp. (small species)

Material: Rębielice Królewskie I: distal end of left tarsometatarsus.

On the contrary to the great homogenity of tarsometatarsi of all Song Birds of Europe, the families *Sittidae* and *Certhiidae* form an exception. There is a more or less deep groove in the middle line of the middle trochlea of the tarsometatarsus, distinctly different in the mentioned two families. On the basis of this feature the bone fragment from Rębielice Królewskie unambiguously belongs to a Nuthatch. The entire bone must have been considerably smaller than that of *Sitta europaea* (see fig. 3).

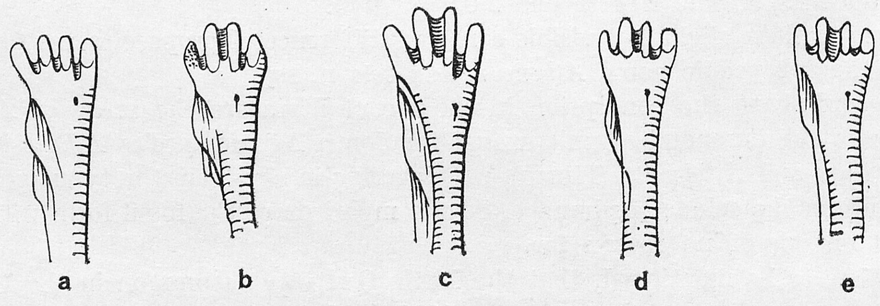


Fig. 3. The sketch of distal part of tarsometatarsus: a — *Certhia familiaris* (recent), b — *Sitta* sp. (fossil from Rębielice Królewskie I), c — *Sitta europaea* (recent), d — *Sitta pusilla* (recent), e — *Sitta canadensis* (recent)

A relation of the remain from Rębielice Królewskie I. to the recent forms of *Sittidae*, according to the present taxonomical conceptions about 20—30 species in the World, is problematic. Small forms of the genus *Sitta* live in Europe only on Corsica (*Sitta whiteheadi* SHARPE) and in the middle and northern parts of Asia and North America: *Sitta europaea asiatica* GOULD from Northern Ural through Sibiria to the Amur; *Sitta neumayer* MICHAHELLES in the Balkans, Asia Minor, through Iran, Irak and Middle Asia and *Sitta canadensis* LINNAEUS with the interesting scattered relict plots of range: Asia Minor and the Caucasus; the Middle Asiatic Mountain area (Tibet, S. Inner Mongolia), Korea, Canada and the Western Part of the U.S.A. According to the majority of authors this last form is conspecific with the Corsican *S. whiteheadi*. A relationship to the zoogeographically distinct forms as South Asiatic small *S. frontalis* (India, Java, Philipine Islands) or the North American *S. pygmaea* is not probable, the more so to the forms from New Guinea, Australia or Madagaskar.

Although it seems not to be very hopeful to compare the remain from Poland with the above listed forms, a relation with *Sitta whiteheadi-canadensis* seems to be the most probable, the identity with these forms can not however be proved.

Family: *Turdidae*

Genus: *Turdus*

Turdus sp.

Material: Rębielice Królewskie I: juvenile left coracoideum, prox. end of left humerus, prox. end of left ulna, left and right carpometacarpus, distal end of a right specimen of the same, distal end of right tarsometatarsus, ungual phalanx.

A detailed comparison of the remains with the corresponding bones of middle sized Song Birds from the European genera *Monticola*, *Turdus*, *Cinclus*, *Sturnus*,

Table XVIII

The measurements (in mm.) of the wing bones of the fossil thrush from Rębielice Królewskie I. compared with recent, similar in size, European members of the genus *Turdus*

Species	Humerus: proximal width	Carpometacarpus: total length
Turdus sp., fossil from Rębielice Królewskie I.	8·2	20.0
Recent birds:		
Turdus philomelos	8·2	18·7
Turdus iliacus	8·3	19·1

Galerida, *Pinicola* and *Oriolus* suggests the closest resemblance with *Turdus*. The shape of the tuberculum mediale, the relation between the pars subtubercularis and supertubercularis fossae anconeae (see JÁNOSSY, 1954), and the form of the caput articulare of the humerus are especially characteristic for the Thrushes in the strictest sense (genus *Turdus*).

The remains are — compared with European species — in the size category of *Turdus iliacus* and *T. philomelos* (see Table XVIII).

Considering the fact, that more than 50 species of genus *Turdus* are known at present in the whole World, it is hopeless to try comparisons with other forms. We must content ourselves with the statement that during the times of Pliocene-Pleistocene boundary a Thrush of the size of the Redwing or Song Thrush was living in the northern parts of Europe.

Genus: *Luscinia*

Luscinia (array of *L. svecica*)

Material: Rębielice Królewskie I: distal end of left tarsometatarsus.

A detailed analysis of the fragment, the comparison with the correspondent bones of the members of the families *Turdidae*, *Sylviidae*, *Muscicapidae*, *Prunellidae*, *Motacillidae*, *Bombycillidae*, *Laniidae* and *Fringillidae* proved a very close resemblance with *Luscinia* (and *Erithacus*), especially with *Luscinia svecica*. However, there are some differences between the fossil fragment and the tarsometatarsus of the Bluethroat i. e. the higher position of the foramen inferior and the facies articularis metatarsalis 1. Therefore the identification cannot be quite sure.

Family: *Motacillidae*

Genus: *Anthus*

Anthus cf. *cervinus* (PALLAS 1811)

Material: Rębielice Królewskie I: distal end of left tarsometatarsus.

As it is well known, even intact bones of *Passeriformes* are hard to determine, more so the fragments. In spite of this fact, I made a very detailed comparison with corresponding bones of the above (at *Luscinia*) mentioned members of Song Bird families. A very close resemblance of the desasibed bone may be found with the *Motacillidae* and among them, especially with the genus *Anthus*. The fragment in size and proportions is, among European forms, nearest to *Anthus cervinus*. The corresponding bones of *Anthus trivialis* and *A. spinoletta* more robust, than our remains.

The fragment is of course not sufficient for further taxonomical conclusions.

As mentioned above, some bone-fragments, chiefly originating from Song Birds, has to be left undetermined. This fragments are as follows:

A larger fragment of a coracoideum (*Turdus?*), two larger and a smaller fragm. of scapulae (one originating from *Charadriidae*), two distal fragm. of humeri of small *Passeriformes*, two larger and one smaller fragm. of ulnae and one of a radius, two larger fragm. of carpometacarpus (*Turdus?*), two smaller fragm. cf tibiotarsus and two larger ones of tarsometatarsus, three phalanges unguae (one, very large of *Corvidae*), one phalanx I digiti 2 alae, small.

III. FAUNISTICAL AND ECOLOGICAL REMARKS

As has been mentioned in the introduction, the „Villafranchian" avifauna of Poland, chiefly that from Rębielice Królewskie, although including only 17 species, seems to be the richest one of that times in whole Europe. In spite of the fact that only 10 % of the whole avifauna of those times are known (the ornithofauna of one confined territory of the temperate zone consists of about 150—200 species today), the relatively large number of *Galliformes* is convenient for further conclusions.

Considering the fact that this is the first record of an avifauna of these times, with a special spectrum („fauna of *Galliformes* dominance"), stratigraphical conclusions may hardly be drawn from it. However, the relatively large number of the first true *Tetraonidae* in Węże and the absolute dominance of Francolins in Rębielice Królewskie seem to be characteristic in contrast to the Tertiary faunae with quite different *Galliformes* (*Paleortyx*-faunas), as well as the Pleistocene faunae with an other composition of *Tetraonidae*. Otherwise, I have to emphasize that the avifauna of Węże is quite different from the geologically nearly contemporaneous locality Csarnóta in Southern Hungary, clearly due to geographical reasons.

The ecological character of the fossil faunas discussed in this paper according to Kowalski (1958, 1960 a and b and verbal communication) and Młynarski (1964) is as follows.

Węże — a forest fauna (with numerous *Cervidae* and *Gliridae*) but also with *Prospalax*, typical steppe-dweller. Desmans are present in smaller number, the larger number of *Insectivores*, as well as *Hypolagus* speak for a milder climate.

Rębielice Królewskie I and II contain a faunal assemblage with numerous Amphibians and Desmans, as well as smaller number of Insectivore species speaking for a slightly colder climate than at the former locality. The average size of the hares is larger, which points in the same direction. Młynarski (1964) found a herpetofauna, which is similar to the Mediterranean carstic faunas of the Balcan Mountains of the present day.

The avifauna of the geologically considerably younger Kadzielnia is so poor that it is unconvenient for former conclusions.

The Tetraonids, as a generally northern group, may indicate at Węże the first wave of „worstening" of the Tertiary climate in the central part of Europe, but still with a rich forest vegetation.

The next step of this process is proved by the first appearance of the unambiguous Arctic element: *Lagopus* together with the likewise northern forest element, *Lemmus*, in Rębielice Królewskie. The greatest problem is the coexistence of *Lagopus* with african-mediterranean elements like the Francolins as well as the recently Mediterranean lizards and snakes (subgenus *Podarcis*, *Coluber viridiflavus*, *Ophisaurus*, *Eryx jaculus*, *Elaphe situla* etc.). This fact may be interpreted in many ways:

1) The northern and southern elements originate from different layers.

2) The two elements were living in vertically different biotops (the first ones in the highland, the second ones in the plains etc.) and the birds of prey brought them together.

3) They were living on the same altitude, but in different biotops (ecological „niches").

The last hypothesis may be the nearest to the reality, because *Francolinus capeki* was surely living together with *Lagopus* also in geologically later times (i. e. in Stránská Skála, Koněprusy etc.). We may include in this discussion the recent observations, which prove a vertical winter-migration in the direction of lower altitudes of female Willow Grouses *L. lagopus* in Northern Europe (Höhn, 1969). At present Willow Grouses live also in the forest-belt (taiga-zone) locally in high moores, far from the proper biotop of these birds, the tundra (Micheyev, 1952), but never in the Mediterranean climate zone.

As regards the climatic significance of the avifauna of Rębielice Królewskie, we must emphasize that except Francolins representing a Tertiary relict as well as *Hieraetus* and perhaps *Athene*, the general character of the assemblage is of a temperate — northern one, and in this fauna *Lagopus* is not a strange form. On the other hand it is obvious, that the ecology of the Grouses of the Pliocene-Pleistocene boundary must have been different from that of recent *Lagopus*.

In this place we have to mention the problem of the origin of the *Tetraonidae* and especially that of the grouses. Among the ornithologists working with recent material, there is a widespred theory that the Tetraonids originated in Northern America. This opinion is based on one hand on the fossil (Tertiary) remains of this group from the American continent, entirely lacking in Europe, on the other hand on the relative large number of recent species of recent *Tetraonidae* on that continent. In opposition to the older data, very early remains of *Lagopus* support the hypothesis that there must have been a separate center of „origin of *Tetraonidae* species of Eurasian type" (*Tetrao* sensu lato, *Lagopus*) at least beginning with the Upper Pliocene, perhaps in Asia, from which all

the grouses of this territory originate. The Eurasian origin is indicated not only by the early appearance of these forms in Europe, but also by the entire lack of *Lagopus* from the Pleistocene of the American continent (according to Brodkorb, 1964, only prehistoric finds of *Lagopus* are known in Alaska, following Wetmore, in Guilday, 1962; Guilday, Martin, Mc Grady, 1964). Below the *Lemmus-Dicrostonyx*-levels only American grouses, as *Pediocetes phasianellus*, *Bonasa umbellus* or *Canachites canadensis* but no *Lagopus* were found. Otherwise, this opinion is justified by the range of the White-tailed Ptarmigan *Lagopus leucurus*, the vacarious form of the Eurasian Ptarmigan *L. mutus*, which agrees well with the range of some mammals of unambiguously Asiatic origin (i. e. the Pika *Ochotona* or the Sagebrush Vole *Lagurus*).

We have to wait for further, stratigraphically well determined finds from Eastern Europe and Asia, before deciding these still open problems of palaeoornithology.

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STRESZCZENIE

Spośród bogatych stanowisk faun pliocenu i starszego plejstocenu w Polsce, zawierających szczątki kręgowców — trzy posiadają mniej lub bardziej liczne szczątki ptaków.

Jednym z nich są Węże I, których wiek, na podstawie wyników badań fauny drobnych ssaków, określony został na okres dolnego wilafranszu. Jest to pierwsza, znana dotychczas w Europie, fauna ptaków z tego okresu. Znalezionych tu 15 fragmentów kości ptaków należy tylko do 4 gatunków: *Tetrao conjugens* n. sp., ?*Lyrurus* sp., *Francolinus* (*Lambrechtia* n. subg.) *capeki wenzenzis* n. ssp. (Pl. I: 7—8) i nie określonego ptaka wróblowatego. Nowy gatunek *Tetrao conjugens* n. sp. (tabela III, Pl. I: 9) ma cechy osteologiczne zbliżone do dwu współczesnych gatunków większych *Tetraonidae* Europy, głuszca i cietrzewia. Plio-plejstoceńskie frankoliny są osteologicznie bardzo bliskie, a równocześnie w pewnych cechach różnią się od współczesnej grupy etiopsko-orientalnej tych ptaków. Została przeto zaproponowana nazwa podrodzaju *Lambrechtia* n. subg. dla wyróżnienia ich od współczesnych form.

Znacznie bogatszą faunę ptaków reprezentują wykopaliska w Rębielicach Królewskich I i II. Z geologicznego punktu widzenia fauna ta jest nieco młodsza

od poprzedniej — pochodzi bowiem ze środkowego okresu wilafranszu. Oznaczalne szczątki ptaków obejmują tu około 330 fragmentów, należących do 17 gatunków (lista gatunków p. s. 532). Fauna ptaków jako całość jest zbliżona do obecnej fauny strefy umiarkowanej Europy, trzeba jednak wziąć pod uwagę, że większość szczątków jest oznaczalna tylko do poziomu rodzaju. Najbardziej rzuca się tu w oczy obecność najstarszych znanych szczątków pardw — *Lagopus lagopus atavus* n. ssp. (Pl. I: 4—8; tabela II), znalezionych w Europie razem z frankolinami, m. in. *Francolinus* (*Lambrechtia*) *minor* n. sp. (tabela XIII; fig. 2) i śródziemnomorskimi jaszczurkami i wężami (wszystkie te gatunki mogą być uznane bardziej za relikty trzeciorzędowe niż elementy „śródziemnomorskie"). Obecność pardw, a także lemingów (*Lemmus*) w Rębielicach Królewskich I. jest najstarszym dowodem pogorszenia się warunków klimatycznych w Europie Środkowej u schyłku pliocenu.

Bardzo uboga fauna ptaków z Kadzielni, zawierająca tylko frankoliny i małą sowę *Glaucidium* sp., odnosi się do górnego wilafranszu, ale nie wystarcza do dalszych wniosków.

РЕЗЮМЕ

Среди богатых стационных распределений фаун плиоцена и нижнего плейстоцена в Польше, содержащих останки позвоночных — три содержат более или менее многочисленные останки птиц.

Одним из них является Венже I. На основании проведенных исследований фауны мелких млекопитающих их возраст определён на период нижнего виляфранша. Это первая, известная до сих пор в Европе, фауна птиц с этого периода. Найденные здесь 15 останков костей птиц принадлежат лишь к 4 видам: *Tetrao conjugens* n. sp., ?*Lyrurus* sp., *Francolinus* (*Lambrechtia* n.subg.) *capeki wenzensis* n.ssp. (Пл.I:7—8) и неопределённой птицы из воробьиных. Новый вид *Tetrao conjugens* n. sp. табл. III, Рис. I: 9) имеет остеологические признаки близкие к двум современным видам больших европейских *Tetraonidae* глухаря и тетерева. Плио-плейстоценские турачи остеологически очень близки и одновременно некоторыми признаками отличаются от современной Эфиопско-Индо-Малайской группы этих птиц. Поэтому, для отличия их от современных форм, предложено название подрода *Lambrechtia* n. subg.

Значительно богаче является ископаемая фауна птиц в Рембелицах Крулевских I и II. Из геологической точки зрения эта фауна незначительно моложе предыдущей — происходит она из среднего периода виляфранша. Определяемые останки птиц здесь охватывают около 330 фрагментов, принадлежащих к 17 видам (список видов см. стр. 532). Фауна птиц в целом похожа к современной фауне умеренного пояса Европы. Однако следует иметь ввиду, что большинство останков можно определить лишь до рода. Наибольше встречается здесь присутствие старейших известных останков белых куропаток —*Lagopus lagopus atavus* n. ssp. (Пл. I: 4—8; табл. II),

найденных в Европе вместе с турачами, между прочим *Francolinus* (*Lambrechtia*) *minor* n. ssp. (табл. XIII; фиг. 2) и средиземноморскими ящерицами и ужами (все эти виды могут быть признаными более третичными реликтами, чем „средиземноморскими" элементами). Присутствие белых куропаток, а также леммингов (*Lemmus*) в Рембелицах Крулевских I является древнейшим доказательством ухудшения климатических условий в Центральной Европе в конце плиоцена.

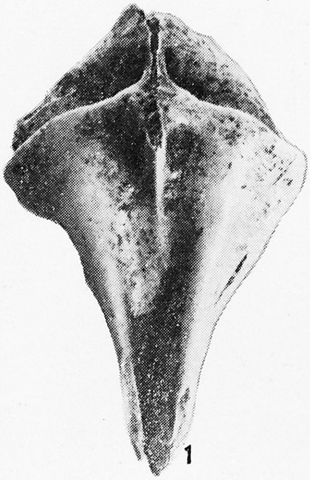
Очень бедная фауна птиц из Кадзельни, содержащая лишь турачей и малых сов *Glaucidium* принадлежит к верхнему виляфраншу, но она не хватает на дальнейшие заключения.

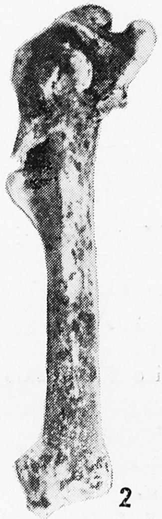
PLATES

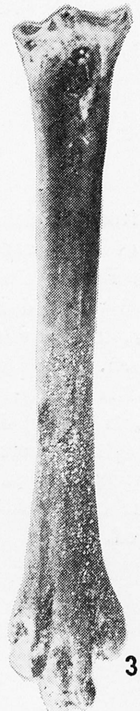
Plate XXIII

Francolinus capeki villanyiensis n. ssp. from Rębielice Królewskie I.:
Phot. 1. Sternum, oral view,
Phot. 2. Left carpometacarpus, ventral view,
Phot. 3. Right tarsometatarsus, anterior view,
Phot. 4. Left humerus, caudal view,
Phot. 5. Left ulna, dorsal view,
Phot. 6. Praemaxilla, caudal view
Francolinus capeki wenzensis n. ssp. from Węże:
Phot. 7. Praemaxilla, dorsal view,
Phot. 8. The same praemaxilla, caudal view.
Tetrao conjugens n. sp. from Węże:
Phot. 9. Proximal end of left carpometacarpus, ventral view.
All photographs are enlarged.

Photographed by G. Szegvári


1

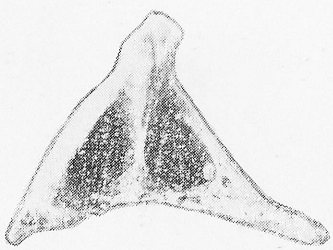

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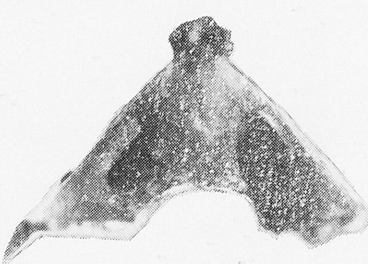

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Plate XXIV

Athene noctua veta n. ssp. from Rębielice Królewskie I.:
Phot. 1. Cranial fragment of left coracoideum, ventral view,
Aquila (*Hieraetus*) sp. from Rębielice Królewskie I.:
Phot. 2. Phalanx II digiti 3 pedis, dorsal view,
Phot. 3. The same phalanx, lateral view.
Lagopus lagopus atavus n. ssp. from Rębielice Królewskie I:
Phot. 4. Fragment of mandibula, ventral view,
Phot. 5. Proximal end of left femur, dorsal view,
Phot. 6. Proximal end of right humerus, cranial view,
Phot. 7. Left carpometacarpus, ventral view,
Phot. 8. Distal end of right tarsometatarsus, dorsal view.
All photographs are enlarged.

Photographed by G. Szegvári



D. Jánossy

Redaktor zeszytu: dr Z. Bocheński

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